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The Unusual Prodissoconch and Larval Development of *Barbatia bailyi* (Bartsch, 1931) (Mollusca: Bivalvia: Arcidae)

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Abstract. In this study, the prodissoconch and developmental mode of the bivalve *Barbatia bailyi* are described for the first time. *Barbatia bailyi* has a large and unusual "hat-shaped" prodissoconch, a form which has appeared only in scattered reports in the literature. Based on observations of live and preserved specimens, this prodissoconch morphology is linked to a non-planktonic, brooded larval developmental mode. This prodissoconch morphology appears in at least two other undescribed species in the genus *Barbatia* (subgenus *Acar*), suggesting that brooded development may be a frequent occurrence in this subgenus.

INTRODUCTION

The morphology of the larval shell, or prodissoconch, can be used to infer important characteristics of bivalve larval development (e.g., Ockelmann, 1965; Jablonski & Lutz, 1980, 1983; Lutz et al., 1980; O'Foighil & Graf, 2000; Malchus, 2000; Malchus & Steuber, 2002). In general, the presence of a distinct prodissoconch II which has prominent commarginal striae indicates that larvae feed in the plankton (that is, they are planktotrophic), while the absence of a distinct and separate prodissoconch II suggests that larvae are non-planktotrophic (Ockelmann, 1965; Carriker & Palmer, 1979; but see Ó Foighil, 1986). Because the length of larval development and hence the dispersal potential of marine species is associated with larval developmental mode (e.g., Thorson, 1950; Jablonski & Lutz, 1983; Strathmann, 1985), the prodissoconch morphology of bivalves can provide valuable clues about the dispersal and early life history ecology of species when the larvae have not been directly observed. This has proven particularly valuable for groups that are difficult to sample, such as bivalves from deep-sea hydrothermal vents, subterranean caves, and the fossil record.

To accurately infer larval developmental mode from the morphology of the prodissoconch, it is first necessary to draw specific connections between prodissoconch morphology and larval development in living species. In some cases this has been difficult because prodissoconch descriptions are much more common and easily obtained than observations of larval development. One example is a type of prodissoconch reported from several bivalve species that is unusual both in its shape and its large size. In recent publications, Kase & Hayami (1992, 1993) and Hayami & Kase (1996) describe a "huge hat-shaped Pd I" on specimens of a newly described arcid species, *Bentharca decorata,* from an unusual cave fauna in the Okinawa Islands of southern Japan. Three other unidentified bivalve species (placed in the taxa *Cosa,* Propeamussiidae, *Limatula*) from the same fauna also had similar prodissoconchs, and another such prodissoconch was described by Barnard (1964:372) on a specimen of "*Arca (Acar) plicata*" from South Africa. Kase & Hayami (1993) suggested that the prodissoconch shape of *Bentharca decorata* indicates non-planktotrophic development and probably parental incubation of juveniles, but because living specimens of this species had not been collected, this relationship could not be directly demonstrated.

In this study, the prodissoconch and developmental mode of the bivalve *Barbatia (Acar) bailyi* (Bartsch, 1931) are described for the first time. Based on observations of living and museum specimens of *B. bailyi,* its unusual "hat-shaped" prodissoconch, similar to that described above for several other species, is linked to a non-planktonic, brooded larval developmental mode. Likewise, this prodissoconch appears in at least two additional undescribed species in the genus *Barbatia,* suggesting that this type of development may be much more widespread in the family Arcidae than previously known.

Barbatia (Acar) bailyi is a member of the bivalve family Arcidae, a large family with a worldwide tropical and subtropical distribution that contains several genera and subgeneric groupings. In the eastern Pacific, the subgenus *Acar* Gray, 1857, ranges from southern California to Peru (Olsson, 1961). Very little is known about the biology and taxonomy of *B. bailyi,* which is a small and inconspicuous species. Compared to other arcids, *B. bailyi* is not abundantly represented in museum collections (personal observation) and is not mentioned in Olsson's (1961) compendium of Panamic-Pacific pelecypods. The name *Barbatia (Acar) bailyi* was first applied by Bartsch (1931) who described the species based on collections by

Figure 1. Numerous *Barbatia bailyi* on the bottom of a rock that was partially buried in coarse sand at the approximately 0 tide mark just south of Newport Beach, Orange County, California. Arrows are pointing to three representative specimens; there are approximately 20 individuals on the rock. Clams are weakly attached to the rock by byssal threads.

A. M. Strong from Balboa, California. This morphological description unfortunately contains few characteristics that can be used to distinguish among *B. bailyi* and other similar arcids with potentially overlapping ranges, particularly the more abundant and somewhat less cryptic *Barbatia (Acar) gradata* (Broderip & Sowerby, 1829). These two species often appear intermixed in museum collections along with *Arcopsis solida* (Sowerby, 1833) probably due to the small size and superficial morphological similarity of all three species. The range extent of *B. bailyi* is at present unclear; museum specimens from as far south as Panama have been identified to this species. Though the northern limits of *B. bailyi* are not currently well established, its presence in Orange County, California (Bartsch, 1931 and herein) makes *B. bailyi* the eastern Pacific arcid with the northernmost distribution of any species in the family.

Microscopic examination of live-collected specimens of *Barbatia bailyi* as well as specimens from the Los Angeles County Museum of Natural History (LACM); the United States National Museum of Natural History, Smithsonian Institution (USNM); and the Naturhistorisches Museum Basel (NMB) revealed that this species has a very large and unusually shaped prodissoconch that can readily be used to distinguish among shells of *B. bailyi* and other species of arcids, and is correlated with brooding of larvae to metamorphosis within the mantle cavity of adults.

METHODS

Live Collections

Live *Barbatia bailyi* were collected on 4 November 2001 and 3 March 2002, just south of Newport Beach, Orange County, California, close to the type locality as described by Bartsch (1931) ("Balboa, Calif."). Specimens were found near the low-tide mark, attached by byssal threads to the undersides of rocks that were partly buried in coarse sand (Figure 1). The clams were patchily distributed, occurring in small groups on the undersides of some rocks (Figure 1) and absent from other adjacent rocks. Animals were brought back live to the laboratory, opened, and gonads were examined under a dissecting microscope. The umbones of the shells of each individual collected were examined to observe the prodissoconch morphology. Shells with intact and clean prodissoconchs were dried at room temperature for later scanning electron microscopy.

Museum Specimens

Specimens labeled "*Barbatia bailyi*" or "*Acar bailyi*" were examined from the LACM and USNM. Other specimens from vials of mixed bivalve specimens labeled as "Arcidae," but morphologically similar to *B. bailyi*, were examined from collections from NMB. Specimens that were examined from the LACM collections included sites at San Onofre, Laguna Beach, Point Vincent and La Jolla (California), San Martín Islands (Baja California, Mexico), and the Gulf of Chiriquí (Panama). Collection localities from USNM included Balboa Beach (California) and Gulf of Chiriquí (Panama). The collection locality from NMB was Edo Carabobo (Venezuela).

Scanning Electron Microscopy

Specimens were prepared for scanning electron microscopy (SEM) by manually removing visible dirt and dust from the prodissoconch region with a soft paint brush, then attaching shells to carbon-adhesive tabs on SEM stubs with the prodissoconch oriented upward and parallel to the surface. Umbonal areas of shells were then examined on a Jeol JSM 6300 scanning electron microscope operated at 15 kV, and images were digitally recorded.

RESULTS

Prodissoconch Morphology

The prodissoconch of the Californian *Barbatia bailyi* is extremely large (396–410 μm in height) and has an unusual inflated, hatlike shape (Figure 2a). It is characterized by a tall peak rising at the umbonal end with a distinctive apical dimple, stellate uneven ribs descending from the raised apex, and a thick, distinct marginal lip which sets the prodissoconch apart from and higher than the dissoconch (Figure 2b). All Californian museum specimens, including specimens from the topotypic lot (USNM 347810), had similarly shaped prodissoconchs. Of the specimens collected live from close to the type locality, approximately 50% had well preserved prodissoconchs. The prodissoconchs of these animals were identical to those pictured in Figure 2b.

Specimens from tropical America (Gulf of Chiriquí, Panama, and Edo Carabobo, Venezuela) were similar in prodissoconch shape to Californian specimens. However, compared to Californian specimens, prodissoconchs from these regions were considerably smaller (250–260 μm) and lacked the dimple at the apical tip (Figures 3a, b; 4a, b). These prodissoconchs were very similar both in size and shape to the larval shells preserved inside the body of one adult specimen (LACM 35-88) from the Gulf of Chiriquí, Panama that was preserved with the valves complete (Figure 5a, foot and body musculature removed). The larval shells were abundant inside the mantle cavity of the adult animal (Figure 5b), and based on size (210–250 μm, close to the prodissoconch heights of adult specimens), these brooded larvae were close to metamorphosis. In Figure 5c the well preserved surfaces of the larval shells can be seen to have a pitted surface over most of the apex, and stellate irregular ribbing running from the base of the peak to the edge of the shell. In Figure 5d, the thickness of the prodissoconch lip can be clearly seen.

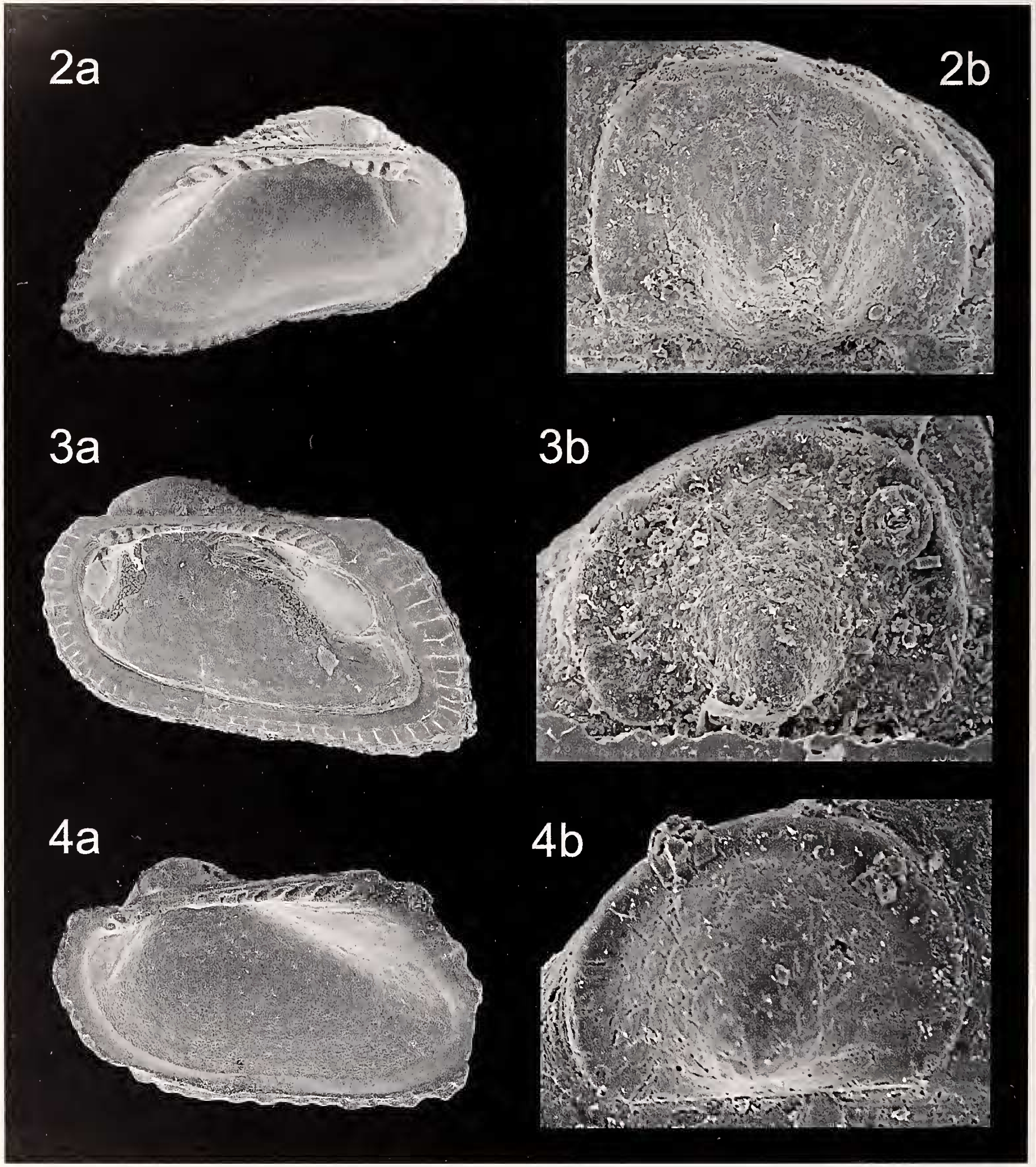
Spawning of Live Specimens

Based on observations of the gonads and spawning behavior of live-collected specimens of *Barbatia bailyi*, this species broods larvae in the mantle cavity to a stage at or close to metamorphic competence. Several females had very enlarged gonads that contained large white oocytes visible through the gonadal wall. One female had spawned recently and contained approximately 50 eggs that were free-floating in the mantle cavity. Spawned eggs had no visible envelope or coat and were round, white, and extremely large; the two longest diameters of 15 measured eggs averaged 216.8 ± 5.9 (SD) and 211.2 ± 5.2 μm. Over the course of 48 hours of observation, eggs underwent the first three cleavages, which were spiral and unequal.

DISCUSSION

The larval shell of *Barbatia bailyi* lacks a prodissoconch II, suggesting that larvae of this species are non-planktotrophic. However, its inflated, hatlike shape is unusual among bivalves and therefore its relationship to larval development is difficult to interpret without further information. The presence of well developed shells of mature larvae in the mantle cavity of a preserved museum specimen, and the very large size and retention within the mantle cavity of the eggs spawned by a female in a live Californian specimen, are strong evidence that this unusual, hat-shaped prodissoconch morphology is associated with brooded larval development as suggested by Kase & Hayami (1993). These observations of brooded larvae and eggs represent one of the first direct observations of brooded development in the family Arcidae.

Additional evidence suggests that this type of development may be relatively widespread within the *Acar* clade. First, the size of the prodissoconch differed greatly (by > 100 μm in length) between the Californian specimens of *B. bailyi* and the Central American nominal *B.*



Figures 2–4. Figure 2a. Specimen of *Barbatia bailyi* from the Strong Collection from southern California, USNM 347810. Figure 2b. Prodissoconch of same. Shell length = 3.0 mm; prodissoconch height = 397 μm. Figure 3a. Specimen of "*Barbatia bailyi*" from the Pacific side of Central America (Gulf of Chiriquí, Panama), USNM 739582. Figure 3b. Prodissoconch of same. Shell length = 4.2 mm; prodissoconch height = 260 μm. Figure 4a. *Barbatia* (*Acar*) specimen from the tropical Western Atlantic (Edo Carabobo, Venezuela), NMB 17675. Figure 4b. Prodissoconch of same. Shell length = 3 mm; prodissoconch height = 230 μm.

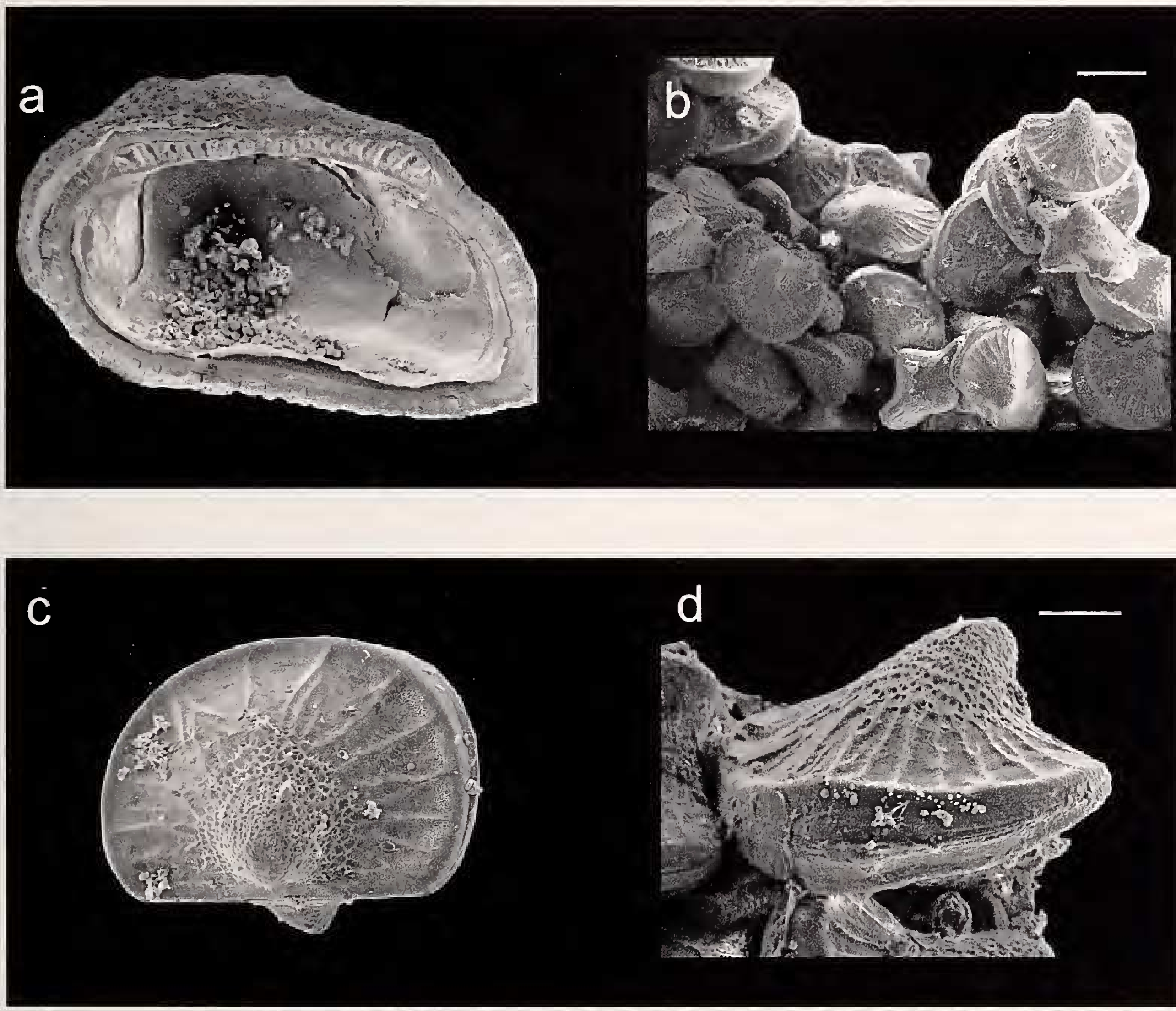


Figure 5. a. "*Barbatia bailyi*" from Central America (Gulf of Chiriquí, Panama), LACM 35-88, opened with foot and body musculature removed; the interior of the mantle lining is still present and contains numerous shells of larvae. Adult shell length = 11 mm. b. View of larval shells inside mantle lining. Scale bar = 180 μm. c. Close-up of a single larval shell from inside the mantle cavity. Shell length = 240 μm d. View of the thickened lip of one larval shell specimen. Scale bar = 60 μm.

bailyi, suggesting that these may be two separate species with similar development but dramatically different sizes at metamorphosis. Alternatively, different prodissoconch sizes could represent divergent developmental modes within a single species, a possibility which could be explored through molecular phylogenetic analysis of nominal *B. bailyi* from different regions.

Second, an ongoing broad survey of prodissoconch morphology in the arcid bivalves (Moran, in preparation) has uncovered specimens from two sites in the Caribbean that also have hat-shaped prodissoconchs similar in shape and size to the central American nominal *B. bailyi.* One of these two specimens is from Venezuela (labeled "Arcidae," NMHB 17675) and the other is from Antigua (labeled *Arca imbricata,* USNM 501720). Both have adult shells with the raised adductor muscle scars typical of the *Barbatia* (*Acar*) subgeneric grouping (Olsson, 1961). Because other described species in the subgenus *Acar* from the Caribbean have planktotrophic development (Moran, in preparation), it is likely that these specimens represent an undescribed species of *Acar* in the western Atlantic. These western Atlantic specimens are very similar in prodissoconch morphology and size (228 and 236 μm height) to the nominal *B. bailyi* from the eastern Pacific of Central America, so it is possible these represent a new pair of "geminate" species within the Arcidae.

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LITERATURE CITED

BARNARD, K. H. 1964. Contributions to the knowledge of South African marine Mollusca. Part 5. Lamellibranchiata. Annals of the South African Museum 47:361–593.

BARTSCH, P. 1931. The West American mollusks of the genus *Acar.* Proceedings of the United States National Museum 80:1–4.

CARRIKER, M. R. & R. E. PALMER. 1979. Ultrastructural morphogenesis of prodissoconch and early dissoconch valves of the oyster *Crassostrea virginica.* Proceedings of the National Shellfish Association 69:103–128.

HAYAMI, I. & T. KASE. 1996. Characteristics of submarine cave bivalves in the northwestern Pacific. American Malacological Bulletin 12:59–65.

JABLONSKI, D. & R. A. LUTZ. 1980. Molluscan larval shell morphology: ecological and paleontological applications. Pp. 323–377 in D. C. Rhoads & R. A. Lutz (eds.), Skeletal Growth of Aquatic Organisms. Plenum Press: New York.

JABLONSKI, D. & R. A. LUTZ. 1983. Larval ecology of marine benthic invertebrates: paleobiologic implications. Biological Reviews 58:21–89.

KASE, T. & I. HAYAMI. 1992. Unique submarine cave mollusc fauna—composition, origin and adaptation. Journal of Molluscan Studies 58:446–449.

KASE, T. & I. HAYAMI. 1993. Submarine cave Bivalvia from the Ryukyu Islands: systematics and evolutionary significance. Bulletin of the University Museum, The University of Tokyo, Vol. 35.

LUTZ, R. A., D. JABLONSKI, D. C. RHOADS & R. D. TURNER. 1980. Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galapagos Rift. Marine Biology 57:127–133.

MALCHUS, N. 2000. Larval shells of Middle Jurassic Oxytomidae (Bivalvia: Monotoidea) from Poland. Journal of Molluscan Studies 66:289–292.

MALCHUS, N. & T. STEUBER. 2002. Stable isotope records (O, C) of Jurassic aragonitic shells from England and NW Poland: palaeoecologic and environmental implications. Géobios 35: 29–29.

Ó FOIGHIL, D. 1986. Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis.* Marine Biology 92:517–524.

Ó FOIGHIL, D. & D. L. Graf. 2000. Prodissoconch morphology of the relict marine paleoheterodont *Neotrigonia margaritacea* (Mollusca:Bivalvia) indicates a non-planktotrophic prejuvenile ontogeny. Journal of the Marine Biological Association of the United Kingdom 80:173–174.

OCKELMANN, K. W. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. Pp. 23–35 in Proceedings of the First European Malacological Congress, 1962. L. R. Cox & J. F. Peake (eds.), Conchological Society of Great Britain and Ireland and Malacological Society of London.

OLSSON, A. A. 1961. Mollusks of the Tropical Eastern Pacific, Particularly from the Southern Half of the Panamic-Pacific Faunal Province (Panama to Peru). Paleontological Research Institution: Ithaca, New York. 574 pp., 86 pls.

STRATHMANN, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16:339–361.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25:1–45.